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REPRODUCTION OF *METRIDIUM MARGINATUM* BY FRAGMENTAL FISSION

M. L. HAMMATT

DURING the autumn of 1897, a specimen of *Metridium marginatum*, about one half an inch in diameter at the base, was kept by the writer for some weeks in a glass jar in an open north window. Its favorite resting place was near the edge of the sea water, where it could be plainly seen both from above and through the side of the glass. One morning it was noticed that its tentacles were withdrawn, that it had evidently moved toward one side, and that whereas the night before its basal outline had been quite regular, it now showed a slight inward curve, opposite to which, at a short distance from it, was a fragment which had evidently been divided off during the night. The separation between the two was not quite complete, as a transparent thread passed from one end of the fragment to the parent form, disappearing, however, soon after. The distance between the two was gradually increased and the fragment was seen to possess life, because it changed shape from time to time.

This fragment was carefully watched for a few days and was seen to curl together gradually until its extremities met, but the opportunity for following its further development was wanting.

Later on it was discovered that this reproduction by fragmental fission in Metridium was mentioned by Verrill in an article entitled "Our Common Sea Anemone" in the second volume of the *American Naturalist*, also that similar reproduction in *Anthea cereus* was noted by Gosse, in *Sea Anemones and Corals*, 1860 (page xxi of the introduction and page 169), and in Tenby, where he states, on page 373: "If the body be torn away and only a portion of the base remain, from this fragment a new offspring will sometimes rise up to occupy the place of its parent." Dicquemare and Dalyell also observed the same mode of division in sea anemones.[1]

When the observation of the writer as above recorded was mentioned to Professor A. Hyatt, he remarked that reproduction by fragmental fission in *Metridium marginatum* had not, to his knowledge, been thoroughly studied and figured, and suggested the advisability of pursuing the investigation further with a view to publication, adding that a series of drawings illustrative of the process observed would be of value as an aid in the teaching of asexual reproduction. In accordance with this suggestion and in the hope of ascertaining whether forms thus produced developed later into whole organisms, more small specimens of the same genus were collected in June, 1898, in the same tidepool from which the former Metridium mentioned had been taken. This tidepool was a small one and in it, especially along the edge, under the overhanging seaweed, the Metridia were numerous. Fragments were sought for and readily found in abundance not far from the mature forms. These were in various stages of the process of curling together and obviously had been produced by fission similar to that already observed within doors. One of these fragments which was larger than the others had partly curled together and on the next day the ends had come in contact and two tiny prominences, apparently the beginnings of tentacles, had appeared.

On examination of this same tidepool at various times since then, like fragments have always been found. They showed generally neither tentacles nor mouth, and their irregular, elongate shape, not having taken on the radiate form, also their brownish color, distinguished them from the transparent young developed from the ovum.[1]

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[1] Since writing the above paper, my attention has been called to A. Andres' publication "Intorno alla scissiparita delle attinie," (*Mitteil. Zool. Sta. Neapel*, vol. 3, pp. 123–148). My observations were made without any previous knowledge of those of Professor Andres or of any other naturalist. They were also made on a different species. Moreover, my figures show three points not illustrated by Professor Andres, or to my knowledge, by any other authority: first, oral views of successive stages of development of the young produced by fragmental fission (laceration) showing the *completion* of the curling process by which the young assumes the parent form; second, serial, transverse sections of parent and young in process of fragmental fission showing the infolding of the body wall preceding the separation of the two; third, diagrams illustrative of the process of such fission.

The Trembley experiments previously performed on the hydra suggested the pursuance of the same method with *Metridium marginatum*, hence on Wednesday, June 15, 1898, at 2 P. M., the fragment figured at Plate 1, Fig. 1, was produced by artificial fission from the base of a specimen one fourth of an inch in diameter. The Metridium threw out one acontium near the mouth and several where it was cut, and drew in its tentacles entirely. When cut off the fragment fell to the bottom of the glass as if it were without life, and had to be turned over with a needle so as to rest on its base. This fragment was kept under careful observation every day for a period of three weeks and, from studies taken from time to time, the accompanying drawings were made.

The lines crossing Fig. 1 (Pl. 1) nearly at right angles to its length represent portions of the radiating mesenteries of the parent form as seen through the body.

At 2.15 P. M. of the same day the Metridium had extended its tentacles, and in the fragment, as seen in Fig. 2 (Pl. 1), the extremities were approaching each other.

Fig. 3 (Pl. 1), drawn at 4.30 P. M. of the same day, shows a nearer approach of the ends and a difference in size, whether due to growth or to the re-assertion of the power of expansion possessed by the normal animal.

In Fig. 4 (Pl. 1), drawn Tuesday, June 21, at 2 P. M., is seen a greater elevation of the column and a more spreading base, although the ends have not yet joined.

In Fig. 5 (Pl. 1) drawn on Wednesday, June 22d, at 10 A. M., the extremities of the fragment have come together, thus producing, approximately, the normal radiate structure of the sea anemone, leaving, however, a slight inward curvature at the point of juncture. The base here is a trifle more extended and the column, as shown in Fig. 6 (the side view of Fig. 5), is much more elevated.

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[1] Since the above observations were recorded, a number of these fragments, already beginning to curl together, have been carefully collected and placed in a jar where the successive stages leading to their maturity have been followed. They have been found to develop in essentially the same way as did the artificially produced fragment described farther on. The ends of one unusually long fragment curled in opposite directions. Could this latter suggest the origin of many of the double-mouthed Metridia found?

On Thursday, June 23d, at 11.30 A. M., Fig. 7 (Pl. 1) was drawn. Here the young form shows translucent prominences afterwards recognized as the beginnings of tentacles, the one at the line of juncture being less developed than the others. This line of juncture is still visible up as far as the tentacles and makes a slight irregularity at the base. The mouth could be discerned but faintly at this time.

Fig. 8 (Pl. 1), the side view of Fig. 7, shows the tentacles more plainly.

Fig. 9 (Pl. 1), represents the young form as it looked on Saturday, June 25th, at 3 P. M. It shows a further development of tentacles and mouth and an increase in size.

In Fig. 10 (Pl. 1), the side view of Fig. 9, the line of juncture is seen to have disappeared throughout the upper third of the column. In Fig. 11 (Pl. 1), drawn on Saturday, July 2d, the hour not noted, this line is still fainter and shorter and a further increase in the size of the animal is indicated. At this time the young Metridium was very active, crawling along the glass at the edge of the water. Ten tentacles were visible, unequal in size. Lack of symmetry is especially noticeable here and in the following figure. This same lack of symmetry holds in all observed forms which were produced by fragmental fission. Whether these forms ultimately become symmetrical is not known to the writer.

Fig. 12 (Pl. 1), was drawn on Wednesday, July 6th, just before the young Metridium was put into formalin. This shows a further growth and a development of two more tentacles, making twelve tentacles in all.

Thus in the three weeks, from Wednesday, June 15th, to Wednesday, July 6th, a fragment from the base of a small *Metridium marginatum* curled together until its extremities met, developed a spreading base, a column, twelve tentacles, and a mouth, and must therefore have performed the nutritive functions, as evidenced also by the increase in the size of the animal. This experiment of artificial fission was repeated several times on other Metridia with similar results.

During the examination of microtome sections of small Metridia at about this time, for the purpose of studying the microscopic structure of the animal, one Metridium revealed the serial sections figured in Plate 2. These figures are slightly diagrammatic, as intended to illustrate merely the point under consideration. From a study of these sections, if the above observation of reproduction by artificial fragmental fission be borne in mind, the inference may be drawn, that at the time of killing, the Metridium from which the sections were taken was preparing to reproduce asexually by cutting off a fragment.

In Fig. 1 (Pl. 2), either the cutting was not parallel to the oral disc, or the column was unevenly distended vertically, as the tentacles are seen on but one side, that opposite to where fission takes place. This is also noticed in sections shown in Figs. 2 and 3 (Pl. 2). The same fact was noted in regard to similarly placed serial sections of other Metridia examined, which were reproducing in the same way.

In Fig. 1 (Pl. 2), the uppermost in which fission is visible, the separation between parent and fragment is seen to be complete. Portions of the old mesenteries reaching from the outer to the inner body wall are visible in this section in the young.

In Fig. 2 (Pl. 2), the fragment cut off is longer than in section 1, but the separation between the two is not quite complete.

In Fig. 3 (Pl. 2), the infolding of the body wall which makes the division between parent and fragment is not continuous as in sections 1 and 2. The break is seen toward that extremity of the body where the tentacles are visible. This break in the continuity of the fold in the section may be due to a slight irregularity in the folding. No separation between parent and fragment, such as was seen in sections 1 and 2, has as yet taken place. The fragment here cuts off a greater proportion of the parent body than in the section before considered. It is also wider and shows longer mesenteries. Bilateral symmetry is here evident in the parent after the infolding of the body wall which is to cut off the fragment. This same fact is noticed in sections of other Metridia in which like fission is taking place.

In Fig. 4 (Pl. 2), the dividing fold is seen pushing inward from either side, evidently about to cut off here a still larger proportion of the parent than in Fig. 3. It will be noticed here, where the ends of these folds are as yet far from meeting that, previous to fission, there has been an increase in size on the side where this is to take place. This seems to be in accordance with the general rule that extra growth usually precedes fission.

Fig. 5 (Pl. 2), shows the folding of the body wall extending inward but little from either end. One of these folds shows new mesenteries growing from the side which is to form the inner surface of the body wall of the parent. In this section the fact is still more apparent that, before fission occurs, the parent form lacks bilateral symmetry and that the division takes place on the larger side.

The same is seen in Fig. 6 (Pl. 2), which shows only the beginnings of the inward foldings of the body wall, after the completion of which the parent form is to be approximately symmetrical.

In the other sections between that shown in Fig. 6 and the base or pedal disk, the same conditions hold with regard to lack of symmetry as related to the side upon which fission takes place. The body wall shows no inward folding here, but judging from the artificial and natural fission observed, the folding would eventually have reached the base.

In all the sections shown, the line *a. b.* passing between the two pairs of directive mesenteries, *d. m.*, represents the plane of symmetry of the parent animal. The fragment is seen to be divided off on one side only of this plane.

The study of serial sections of other Metridia showed the complete and the partial infolding of the body wall essentially like the above, and evidently preceding fragmental fission.

In consideration of the facts as observed and stated above, the following conclusions are reached by the writer as to asexual reproduction in *Metridium marginatum* by fragmental fission. This occurs in nature as observed in the jar within doors and as seen in the tidepools; also as indicated by the sections. It occurs frequently, as shown also by observations on tidepools.

From the study of sections it is inferred, that the body becomes bilaterally asymmetrical before fragmental fission takes place, this occurring always, as far as observed, on the larger side and that the fragment thus cut off includes body wall (formed on the side next the parent by infolding of the parent body wall), and parts of directive and other mesenteries on one side only of the plane of symmetry of the parent animal. The sections show also that the infolding of the body wall proceeds gradually, and simultaneously downward and inward from the top and upper part of the sides, and that separation of the fragment from the parent commences at the top, as indicated by diagrams (Figs. 7 and 8, Pl. 2).

This infolding of the body wall here, to separate the fragment from the parent form, seems to be essentially the same process as the constriction which divides the Hydra bud from its parent, but here the basal attachment modifies the process by preventing the infolding on that side and by keeping the fragment close to the parent until separation is complete. Whereas in Hydra, a thread tied between parent and bud would represent the method of division, in Metridium the thread may be imagined as held down at either side of the pedal disk and gradually tightened along the line which is to separate parent from fragment, thus producing an infolding proceeding downward from the top and inward from the upper part of the sides.

Observations of the young naturally and artificially produced by fragmental fission show that the fragment cut off curls together until its extremities meet, making parts of mesenteries before nearly parallel now radial in arrangement, thus attaining to the sea anemone structure with the least possible expenditure of energy. From artificial fragmental fission principally, it is seen that the base or pedal disk spreads for attachment, the column becomes elevated, the line of juncture tends to disappear, mouth and tentacles develop, and growth in volume apparently takes place; that the young thus produced, possesses the power of locomotion and that it is, in fact, a whole organism, and, except for the fact that it has not yet attained symmetry, is essentially, in outward appearance at least, a smaller reproduction of its parent.

Obligations are due to Dr. A. G. Mayer for reading this paper, to Mrs. J. M. Arms Sheldon for valuable suggestions, and to Professor G. H. Parker for the determination of specimens; also to the artist, Mrs. A. M. Dodge, for faithful delineation of specimens and sections.

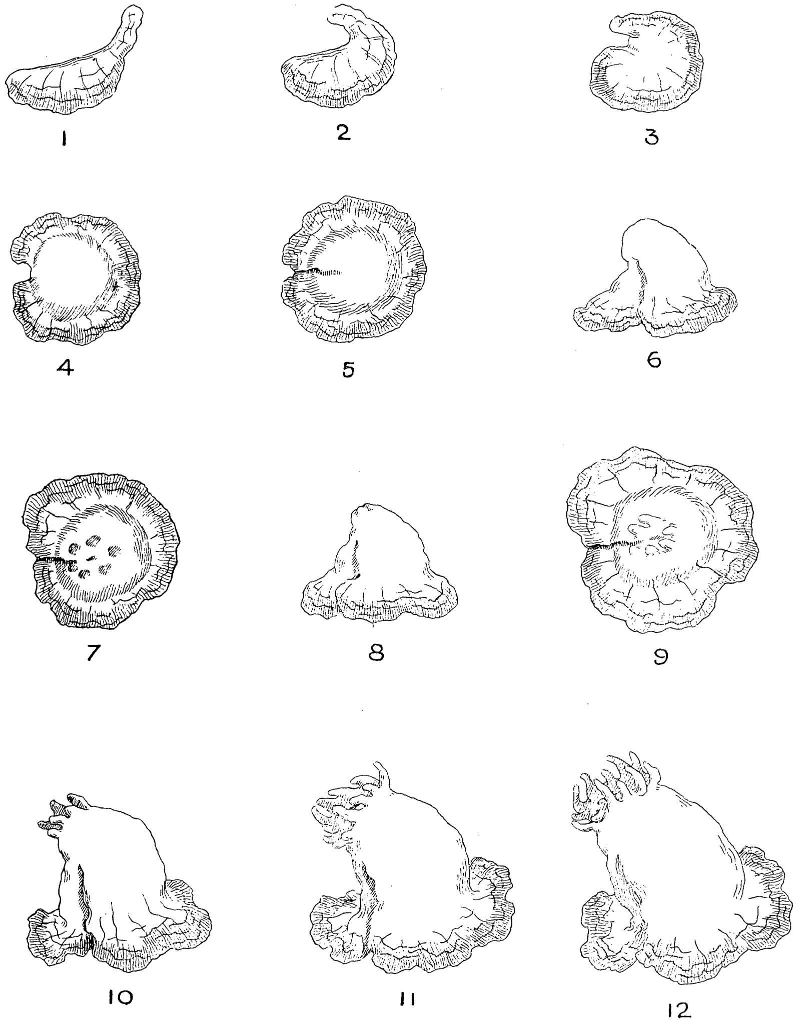

PLATE 1.

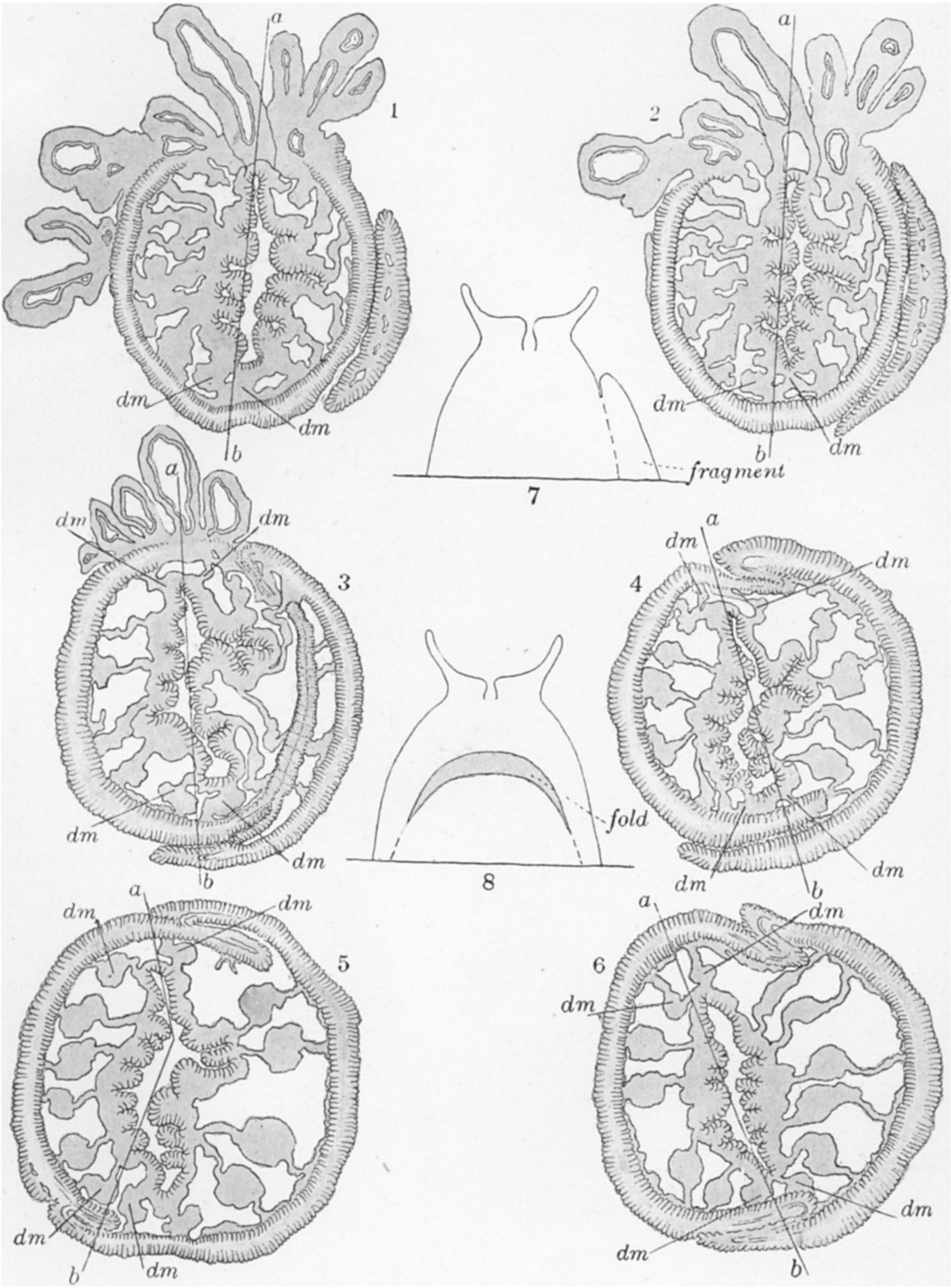
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PLATE 2.